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# A CONTRIBUTION

TO THE

# Morphology of the Medulla Oblongata of the Rabbit

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BY

FRANKLIN DEXTER, M.D.
Assistant Professor of Anatomy, Harvard University

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BOSTON
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1896

# A CONTRIBUTION TO THE MORPHOLOGY OF THE MEDULLA OBLONGATA OF THE RABBIT.

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We owe a large proportion of our knowledge relating to the development of the human spinal cord and medulla oblongata to the researches of His and Cajol. Most of these were made on the human embryo.

It seemed to me that it would be interesting if their results could be verified in the rabbit. To my surprise, I found that the development of the medulla of the rabbit differed from the human in several respects. Before describing these differences, it might be well to recapitulate briefly some of the salient points in the development of the human medulla.

At an early stage in the development of the human spinal cord, its central canal might be diagrammatically described as being somewhat diamond-shaped. (Fig. 1.)

Minot has proposed to designate the different divisions of its wall as the zones of His. He divides them into two dorsal (Flügelplatte) and two ventral zones (Grundplatte), a roof (Deckplatte) and floor plate (Bodenplatte).

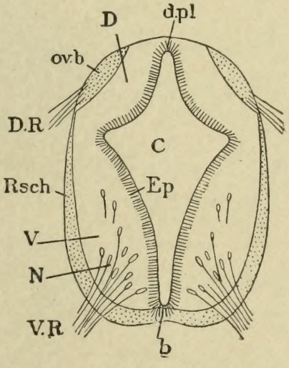

Fig. 1.

(Minot, 346.) Diagrammatic section of the embryonic spinal cord. *dpl*, deck-plate. *D*, dorsal zone. *ovb*, oval bundle. *DR*, dorsal root. *Rsch*, Randschleier. *V*, ventral zone. *N*, neuroblasts. *VR*, ventral root. *b*, bodenplatte. *C*, central canal. *Ep*, ependymal layer.

The two dorsal zones unite by the obliteration of that part of the medullary canal which separates them, and as a result of this union the future posterior septum of the adult spinal cord is formed.

The portion of the medullary canal which is bounded by the two ventral zones remains throughout life as the central canal of the cord.

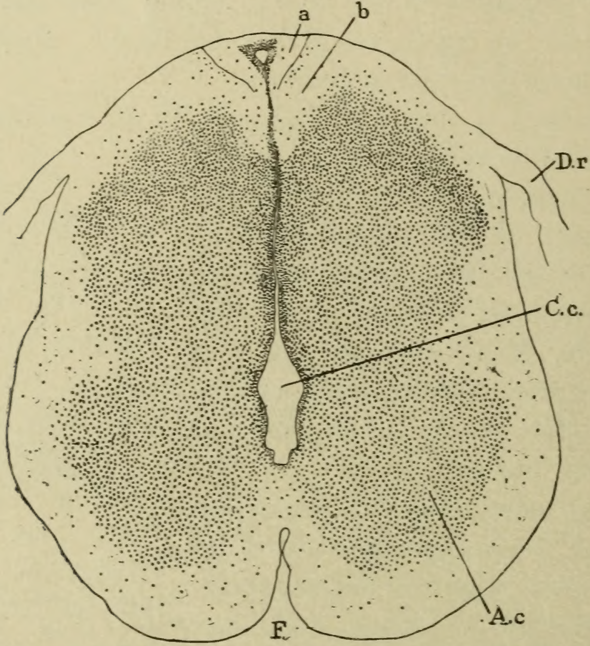

Fig. 2.

(Minot, 376.) Section of the spinal cord of a human embryo of sixty-three to sixty-eight days. Minot Coll., No. 138 (Dorsal region). *a*, Goll's cord. *b*, Burdach's cord (Keilstrang). *Dr*, dorsal root. *Cc*, central canal. *Ac*, anterior cornu. *F*, anterior fissure.

The medullary substance of the two ventral zones increases rapidly, and in such a manner as to leave a space between them. This space corresponds to the anterior fissure of the adult cord. (Fig. 2.)

Thus, in a general way, the morphology of the spinal cord is explained.

The medullary wall may be divided into three layers, the ependymal or inner neuroglia layer, the Randschleier or outer neuroglia layer, and between the two the gray or mantel layer.

The ependymal layer in the adult is represented by the epitheliod cells lining the central canal of the cord.

The Randschleier corresponds to the white substance of the adult cord, and is deficient in nerve cells.

The gray or mantel layer is that which lies between the other two, and it is only in this layer that nerve cells are to be found.

There are two principal types of nerve cells, and these differ materially from each other: 1. The Golgi type. 2. The Deiter type.

The Golgi are found chiefly in the posterior horns of the gray matter, and their neuraxons, or axis cylinders, do not leave the nervous system, but act within it as commissural fibres.

I here use the term Golgi type in its broadest sense.

The Deiter type, on the other hand, is only present in the anterior horns of the gray matter, and their neuraxons leave the nervous system, and invariably by way of the ventral zones. After their exit from the medullary wall, they form the anterior nerve roots, or, as they were formerly called, the motor roots of the spinal nerves. So we see that an anterior nerve root is composed of fibres derived from Deiter's cells, which leave the medullary wall by means of the ventral zone.

The posterior or sensitive nerve roots have a totally different history.

Before the closing of the medullary groove, certain large and well-defined ectodermic cells are easily distinguishable at the point where the skin layer of the ectoderm is about to separate from the closing medullary groove. These cells leave the medullary wall, and wander external to it within the mesoderm, and there unite to form the so-called anatomical ganglion of the spinal nerves. (Fig. 3.)

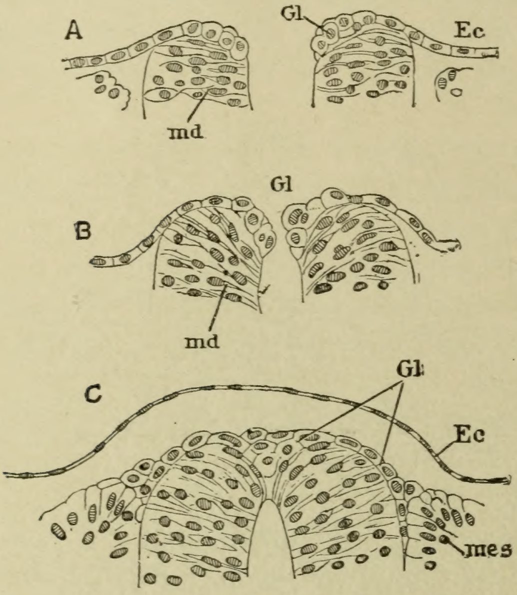

Fig. 3.

(Minot, 344.) Sections through the cervical part of the medulla of a human embryo, with thirteen segments. *A*, in front of the segments where the medullary groove is widely open. *B*, a little further back, where the medullary groove is just closing. *C*, at the level of the third segment. *Ec*, ectoderm. *Gl*, ganglionic anlage. *Md*, medullary wall. *Mes*, mesoderm. After Leuhossek.

Each cell is spindle-shaped and gives off two processes :

One which grows outward and which is joined by the anterior nerve root — the two forming a spinal nerve. The second process grows inward, and enters the Randschleier of the cord in the dorsal zone, close to the boundary of the ventral. It then divides, its fibres running up and down the cord.

In a transverse section of the medullary canal, these fibres are seen forming the so-called oval bundle, which in the adult corresponds to the columns of Burdach, as well as to the posterior columns of the cord.

Hence it is apparent that the origins of the motor and sensitive nerve roots of the spinal cord are totally different. The former originate within the central nervous system and leave it by means of the ventral zone. The latter take their origin outside of the central nervous system and enter it through the dorsal zone.

It is not to be wondered at that the functions of these two sets of fibres should differ so materially from each other; since they have such totally different origins.

If we now compare the development of the medulla with that of the cord, we shall find that it differs in four salient particulars:

1st. The widening of the roof.
2d. The ventral zones come to lie in one plane.
3d. The development of the rhomboidal lip.
4th. Formation of the raphé.

It was shown in the development of the spinal cord that the cavity between the dorsal zones became obliterated, and thus the posterior septum was formed.

In the medulla the reverse of this process takes place.

The dorsal zones become widely separated from each other, and as a result of this the roof plate is very much widened. (Fig. 4.) The central canal presents a five-sided figure. The same process continues, the dorsal zones grow farther and farther apart, until the ventral zones come to lie in nearly the same plane.

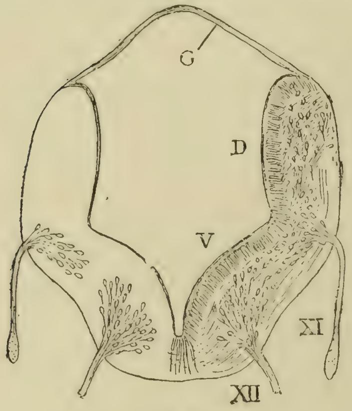

Fig. 4.

(Minot, 374.) Section of the medulla oblongata of a five weeks' human embryo. (His's Ko.) *D*, dorsal zone of His. *V*, ventral zone. *XI*, accessorius. *XII*, hypoglossus. After W. His.

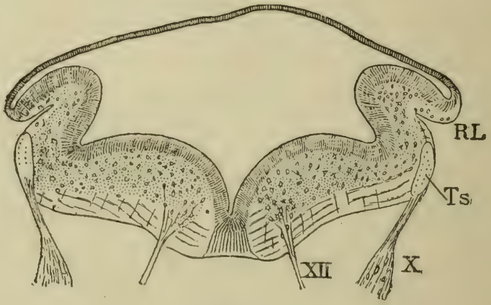

Fig. 5.

(Minot, 379.) Transverse section of the medulla oblongata of His's embryo. *Ru* (Nackenlänge 9.1 mm.), after W. His. *RL*, Rautenlippe. *Ts*, tractus solitarius. *X*, vagus nerve. *XII*, hypoglossal nerve.

The oval bundle (which is now known as the tractus solitarius, as identified by His) can be seen in the Randschleier of the dorsal zone.

It is here formed by the posterior nerve roots of the IX and X nerves, which are homologous to the sensitive roots of the spinal nerves. (Fig. 5.)

At the junction of the roof with the dorsal zone, the rhomboidal lip is developed. These two lips grow downward, or, more accurately, forward, and meet in the middle line. The result of this is, that the tractus solitarius becomes buried by their growth, and their meeting in the middle line forms the so-called raphé of the medulla. (Fig. 6.)

In the adult medulla the division line between the dorsal and ventral zones is indicated by the superior and inferior fovea, but in the regions where they are deficient, it can always be approximately determined by the position of the tractus solitarius, which, it must be remembered, lies within the dorsal zone, close to the boundary of the ventral.

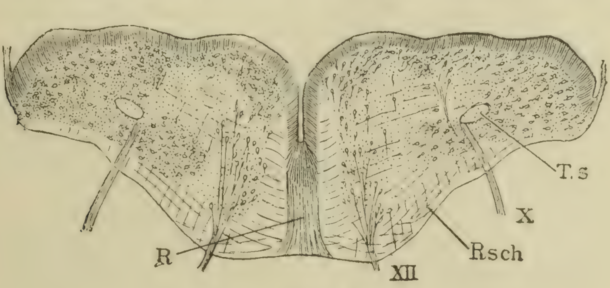

Fig. 6.

(Minot, 381.) Section through the medulla oblongata of His's embryo *CR*. *Ts*, tractus solitarius. *X*, vagus nerve. *Rsch*, Randschleier. *XII*, hypoglossal nerve. *R*, raphé. After W. His.

These are, for our purposes, the salient points in His's description of the development of the human medulla.

I find that the development of the medulla of the rabbit differs from this description in three particulars:

1st. The tractus solitarius is formed from the V (VII and VIII), IX, and X nerves.

2d. The oval bundle and tractus solitarius are probably not completely homologous.

3d. A total absence of the rhomboidal lip.

## Formation of the Tractus Solitarius.

In carrying out this investigation I made serial sections of over fifty embryo rabbits. These varied in length from 6 to 18 mm., and the sections from 3 to 17 $\mu$ in thickness. They were invariably stained with eosine and cochineal. The drawings are all compound figures, taken, as the case may be, from three to perhaps twenty of the sections. They were in each case drawn with a camera lucida.

Two embryos were chosen 10.8 mm. long, and serial sections were made of each. One was cut parallel to the floor of the fourth ventricle and the other at right angles to it. I mean by the floor of the fourth ventricle that portion of it which is situated between the bend of the pons Varolii and the neck-bend of the medulla.

A section taken from the former of these series is shown in Fig. 7. The ectoderm is represented by fine dots in contradistinction to the mesoderm, in which the dots are placed farther apart. The tissue of the Randschleier has not been drawn in, but is represented by a space at the edge of the ectoderm, next to the mesoderm. The finely drawn lines, in all cases, denote nerve fibres.

On examination of this section, we see the cavity of the fourth ventricle cut longitudinally, nerve fibres situated in both the Randschleier and medullary wall, and moreover the V (VII and VIII) ganglia as well as small portions of the IX and X. The otic vesicle is also present, and three separate portions of the jugular vein.

If we examine closely the nerve fibres derived from each ganglion, we find that there are some from the V which enter the Randschleier, but which do not penetrate into the medullary wall. These fibres are reinforced by others from the (VII and VIII) ganglia, and below this point certain fibres are found within the medullary wall, as well as in the Randschleier.

In a section of this kind it cannot be determined whether the former (within the medullary wall) are derived from the V or (VII and VIII) ganglion. It will be seen later, when we examine the cross-sections of this region, that they are really derived from the latter. This band of fibres, from the (VII and VIII) ganglia, enters the medullary wall, and joins a tract which is derived from the posterior nerve roots of the IX and X ganglia, and which is commonly known as the tractus solitarius.

Certain other nerve fibres, derived from the

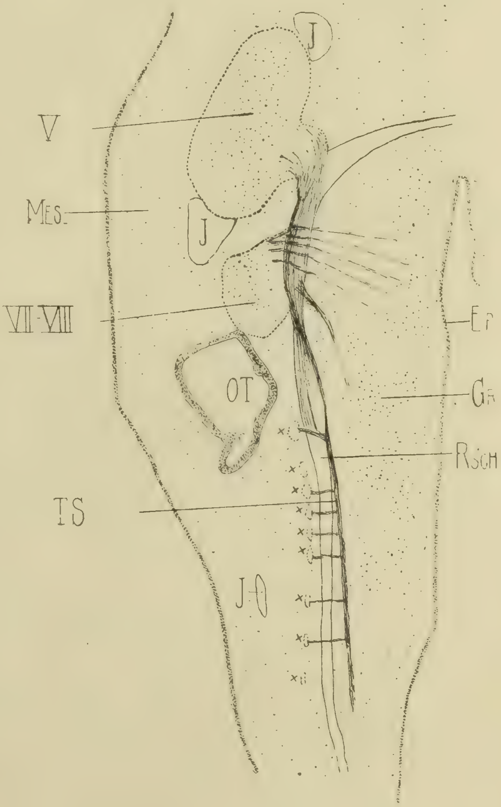

Fig. 7.

Section of the medulla of an embryo rabbit 10.8 mm. parallel to the floor of the fourth ventricle. *V*, ganglion. *VII*, *VIII*, ganglia. ×, sections of the IX and X ganglia. *TS*, tractus solitarius. *OT*, otic vesicle. *J*, jugular vein. *Mes*, mesoderm. *Ep*, ependymal layer. *Gr*, gray layer. *Rsch*. Randschleier.

(VII and VIII) ganglia, can be seen extending across the medullary wall. Exactly what these are it is difficult to determine, but it is possible that they may be the developing striæ acusticæ.

If we now turn our attention to sections cut at right angles to the floor of the medulla, at points corresponding to the position of each ganglion, we shall find that they would agree with the longitudinal section.

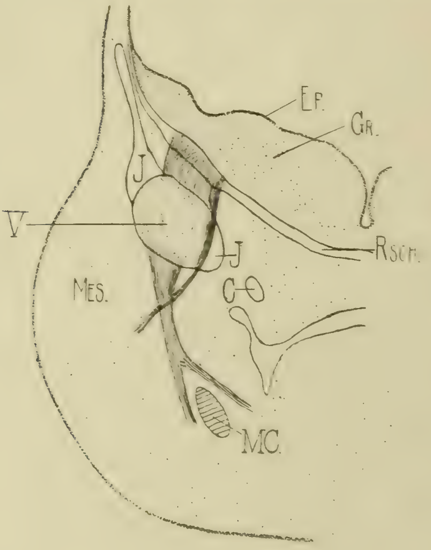

Fig. 8.

Section of the medulla of an embryo rabbit 10.8 mm. at right angles to the floor of the fourth ventricle in the region of the V ganglion. *V*, ganglion. *Ep*, ependymal layer. *Gr*, gray layer. *Rsch*, Randschleier. *Mes*, mesoderm. *J*, jugular vein. *C*, carotid. *MC*, Meckel's cartilage.

Figure 8 shows such a section of the V ganglion. The medullary wall is again represented by the fine dots and bounded externally by the Randschleier, the space between lines, and still more externally by the coarsely dotted mesodermic tissue. The pharynx, internal carotid artery, and jugular vein appear in section, and the irregularly shaped V ganglion is seen within the mesoderm. One set of nerve fibres extends from the ganglion to the Randschleier, but does not enter the medullary wall; the others extend downward until they meet Meckel's cartilage, and there divide. On the inner side of the ganglion certain fibres are seen extending from the Randschleier outward. These probably correspond to the lateral root of this ganglion.

Figure 9 is a drawing of a transverse section of the (VII and VIII) ganglia.

The pharynx, carotid, and jugular vein are seen as before, but the ganglia are more complicated.

The two divisions of the VIII ganglion, the vestibular and cochlea, are separated from each other. Inferior to the latter a small piece of the cochlea appears in section. Between these two ganglia the motor root of the VII appears, whose fibres can be seen arising from the ventral zone of the medulla, crossing the Randschleier, and then becoming indistinct in their relation to the geniculate ganglion.

In this preparation, no fibres could be traced from the cochlear ganglion to the medullary wall. The vestibular ganglion is of an irregular pear-shape, and fibres can be seen extending from it across the Randschleier and into the medullary wall. These fibres correspond to those already described in

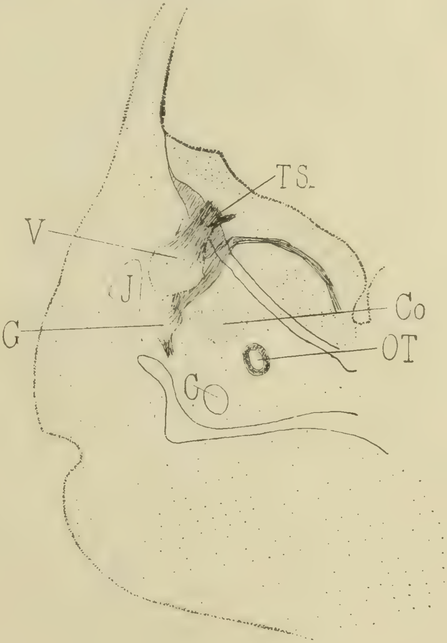

Fig. 9.

Section of the medulla of an embryo rabbit 10.8 mm. at right angles to the floor of the fourth ventricle in the region of the (VII, VIII) ganglia. *TS*, tractus solitarius. *V*, ganglion vestibuli. *G*, ganglion geniculi. *Co*, ganglion cochleae. *J*, jugular vein. *C*, carotid. *OT*, otic vesicle.

Figure 7. They are situated within the medullary wall, opposite the otic vesicle, and are continuous with the tractus solitarius.

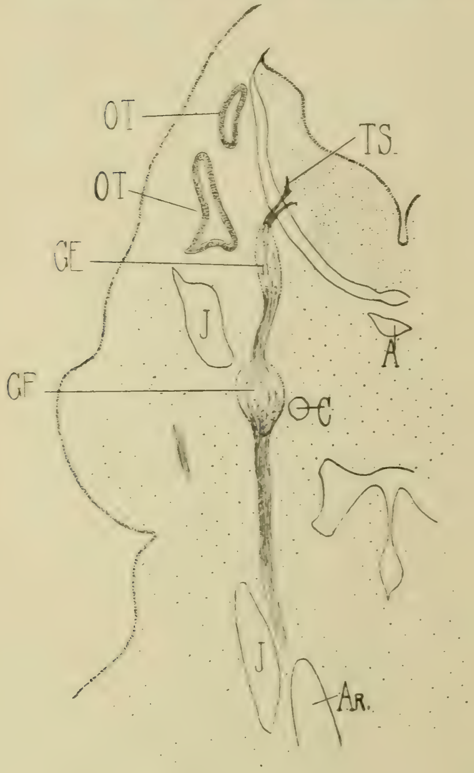

Fig. 10.

Section of the medulla of an embryo rabbit 10.8 mm. at right angles to the floor of the medulla, in the region of the IX ganglia. *TS*, tractus solitarius. *OT*, otic vesicle. *GE*, Ehrenritter's ganglion. *GP*, ganglion petrosum. *A*, aorta. *J*, jugular vein. *C*, carotid.

In figure 10 we have a transverse section of the medulla at the level of the IX nerve.

This drawing shows the pharynx, aorta, internal carotid, and jugular vein in cross-section, as well as portions of the otic vesicle; but the salient point for us is the relation of the IX ganglion. This is plainly seen, with its two divisions, Ehrenritter's ganglion and the ganglion petrosum.

Two sets of nerve fibres are in relation with the medullary wall. The inner is probably the lateral root of the IX nerve, rising from the ventral zone of the medulla.

The external is the posterior root, entering the medullary wall previous to its division to aid in the formation of the tractus solitarius.

The two ganglia are connected by nerve fibres, and others are seen extending downward, internal to the jugular vein.

Figure 11 is a transverse section of the X ganglion, and at a superficial glance does not differ materially from that of the IX.

Its two ganglia, the jugular and nodosum, are quite characteristic and larger in size than those of the IX. The posterior nerve root from the ganglion jugulare enters the medullary wall before its division to join in the formation of the tractus solitarius, and the lateral root is also present, as in the former section.

If we now compare Figure 7 with a similar section of an older embryo, one which measures 13.6 mm. in length, as is shown in Figure 12, we shall find several differences; but most of them relate to the degree of development of nerve fibres. In this

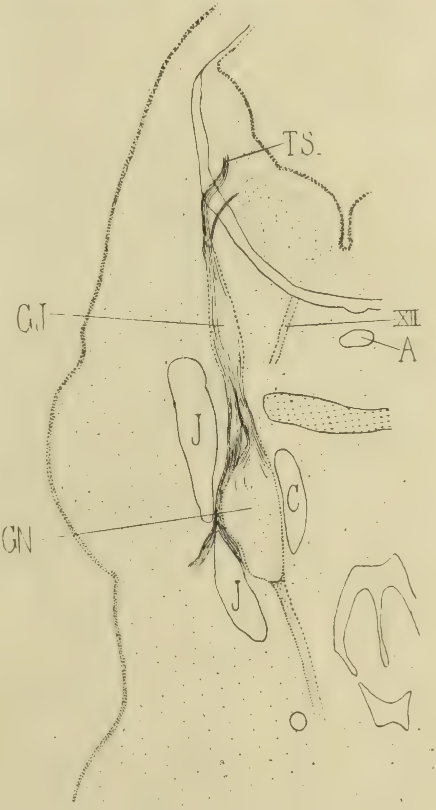

Fig. II.

Section of the medulla of an embryo rabbit 10.8 mm. at right angles to the floor of the medulla, in the region of the X ganglia. *TS*, tractus solitarius. *GJ*, ganglion jugulare. *GN*, ganglion nodosum. *XII*, hypoglossal nerve. *A*, aorta. *J*, jugular vein. *C*, carotid.

section, too, fibres can be seen coming from the V ganglion and completely filling the Randschleier; but there are others, which enter the medullary wall, and running downward help to form the tractus solitarius.

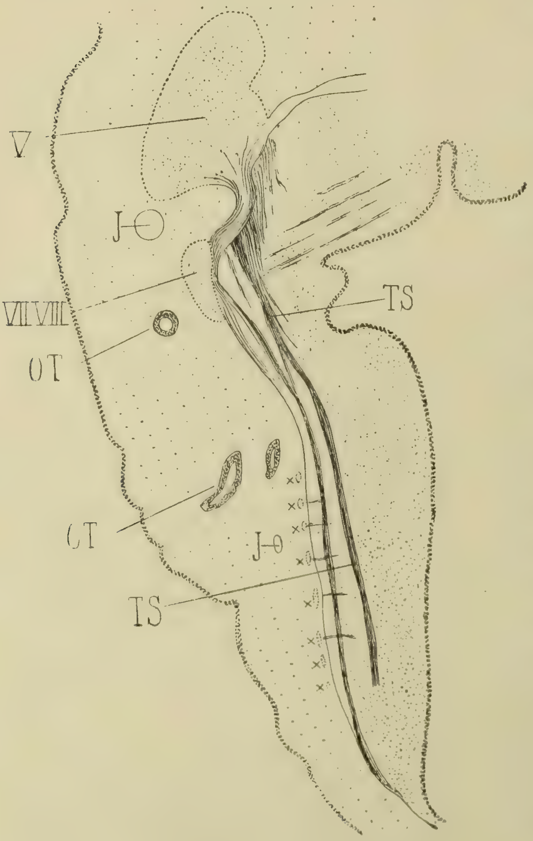

Fig. 12.

Section of the medulla of an embryo rabbit 13.6 mm. parallel to the floor of the fourth ventricle. *V*, ganglion. *VII*, *VIII*, ganglia. ×, sections of the IX and X ganglia. *J*, jugular vein. *OT*, otic vesicle. *TS*, tractus solitarius.

It will be observed that these fibres are absolutely wanting in Figure 7. This simply means that they are developed at a later date; for they are certainly very distinct in Figure 12, which is an older embryo. Others join fibres derived from the (VII and VIII) ganglia, which likewise descend in the medullary wall, external to the tractus solitarius and close to the Randschleier. These fibres probably correspond to the so-called ascending trigeminal tract. It will also be noticed that the bundle forming the tractus solitarius is larger in size than in the younger embryo. This is of course due to the increase of nerve fibres. Moreover, it is much more deeply situated within the medullary wall than in the younger embryo.

Portions of the IX and X ganglia are seen in section, but one fails to follow nerve fibres arising from them as far inward as the tractus solitarius.

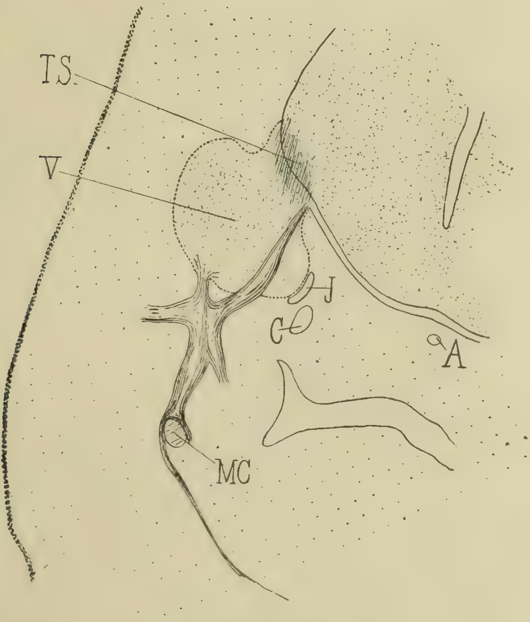

Fig. 13.

Section of the medulla of an embryo rabbit 14 mm. at right angles to the floor of the fourth ventricle in the region of the V ganglion. *V*, ganglion. *TS*, tractus solitarius. *A*, aorta. *J*, jugular vein. *C*, carotid. *MC*, Meckel's cartilage.

If we now make a section transverse to the floor of the medulla, of an embryo of about the same age as in Figure 12, we shall find what is represented in Figure 13.

The chief point of difference between this embryo and Figure 8 consists in the entrance of the nerve fibres derived from the V ganglion into the medullary wall. It is here that these fibres enter into the formation of the tractus solitarius. The remaining fibres have increased very much in size, through the growth of the embryo, — indeed, an entirely new branch of this nerve is seen.

Figure 14 represents a similar section made through the (VII and VIII) ganglia of an embryo 14 mm. in length. This section differs materially from that of the younger embryo shown in Figure 9. The fibres derived from the vestibular ganglion can be followed much deeper into the medullary wall, to form the tractus solitarius, than in the section of the younger embryo.

This corresponds with the position of the tractus solitarius, in the sections cut parallel to the floor of the medulla in the 13.6 mm. embryo. Moreover, fibres from the ganglion cochlearis (which were entirely absent in Figure 9) cross the root of the geniculate ganglion and unite with fibres derived from the vestibular.

This being the case, I am unable to state with certainty whether fibres derived from the vestibular, cochlea, or geniculate ganglia all enter into the formation of the tractus solitarius, or whether one set alone aids in its formation. Should this last supposition be correct, judging from the preparations it would seem to me most likely that they were derived from the ganglion vestibularis.

Transverse sections of the nerve roots of the IX and X ganglia of this same embryo failed to show anything of importance relating to our subject.

On comparing these sections with each other, it seems to me that there can be no doubt that in the embryonic rabbit the tractus solitarius is formed by nerve fibres derived from the posterior nerve roots of the V (VII and VIII), IX, and X ganglia.

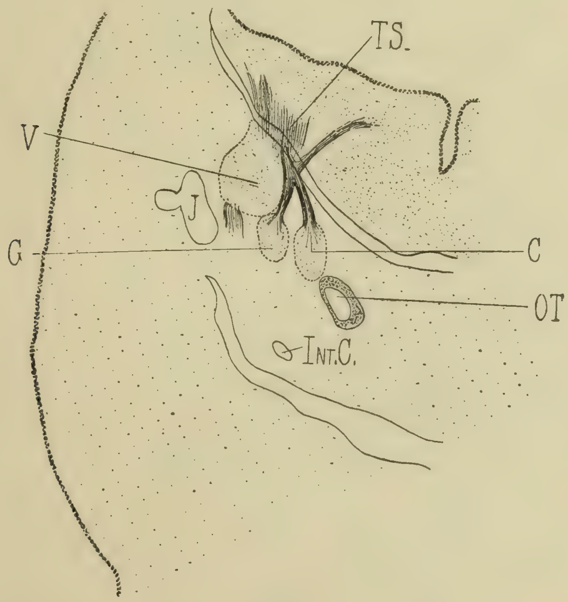

Fig. 14.

Section of the medulla of an embryo rabbit 14 mm. at right angles to the floor of the fourth ventricle in the region of the VII and VIII ganglia. *V*, ganglion vestibuli. *G*, ganglion geniculi. *C*, ganglion cochleae. *TS*, tractus solitarius. *OT*, otic vesicle. *Int C*, internal carotid. *J*, jugular vein.

Thus the tractus solitarius is rendered a much more important structure than has been previously assumed, since more nerve fibres enter into its formation. This fact, moreover, demonstrates the great similarity which exists between the four great cranial ganglia — the V (VII, VIII), IX, and X — a fact which hitherto has only been held as a supposition.

## The Relation of the Oval Bundle to the Tractus Solitarius.

The exact relation of the oval bundle to the tractus solitarius is difficult to determine. I do not in the rabbit consider them as homologous, on account of the difference in their position; although portions, at least, of their fibres are continuous with each other.

The oval bundle is invariably found in the Randschleier of the spinal cord; the tractus solitarius invariably in the gray or mantel layer of the medulla.

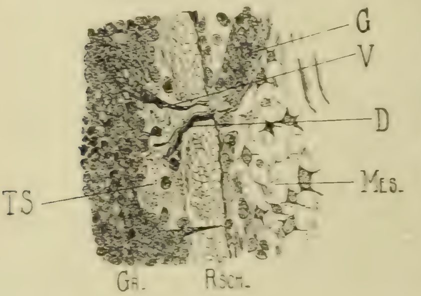

Fig. 15.

Section of the medulla of an embryo rabbit 8 mm. at right angles to the floor of the fourth ventricle in the region of the IX ganglion, and seen under an oil immersion. *Gr.* gray layer. *Rsch.* Randschleier. *Mes.* mesoderm. *G.* ganglion. *V.* lateral root. *D.* dorsal root. *T.S.* tractus solitarius.

In a rabbit embryo of less than 8 mm. in length, the nerve fibres are not sufficiently developed to allow one to follow them.

Figure 15 is a transverse section of the medulla of a rabbit embryo 8 mm. in length, drawn under an oil immersion. The nerve fibres are poorly developed, but can be seen leaving the ganglion of the IX nerve. They enter the medullary wall, divide, and contribute to the formation of the tractus solitarius. It will be observed that this is situated within the boundary line of the mantel layer, as are also a few ectodermic cells, which separate it from the Randschleier.

It is an undoubted fact, as has already been stated, that the depth of burial of the tractus solitarius depends on the age of the embryo. The older the embryo, the deeper it is buried within the medullary wall. At the same time, I have in no case been able to find it in the Randschleier. This leads me to suppose that the oval bundle and tractus solitarius are not homologous. That at least a portion of the oval bundle is continuous with the tractus solitarius cannot be doubted.

Figure 16 represents the tractus solitarius in its course through the medullary wall of the medulla. On the one hand, it is seen connected with the oval bundle of the cord, and it will be particularly observed that it is here situated in the Randschleier. On the other hand, it can be followed until the bend of the medulla gives us its fibres in cross-section (*TS′*).

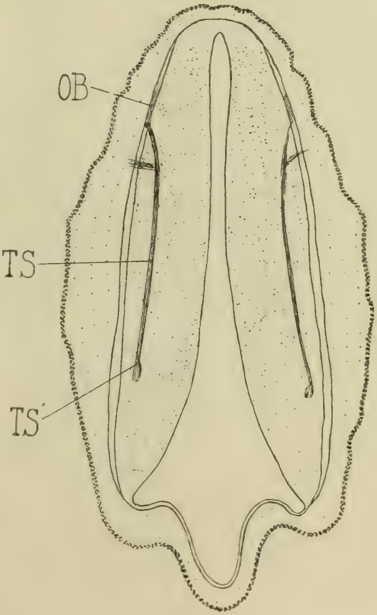

Fig. 16.

An oblique section of the lower region of the medulla and the cervical region of the spinal cord of an embryo rabbit 11.2 mm. *OB*, oval bundle. *TS*, tractus solitarius. *TS′*, fibres of the tractus solitarius in cross-section.

### The Rhomboidal Lip.

In all the transverse sections of the medulla of embryonic rabbits that I have made, I have in no case seen any sign of the rhomboidal lip. This was a very great disappointment to me, for certainly nothing can be more beautiful than His's description of the morphology of the human medulla oblongata.

I am convinced, however, that in the rabbit the medulla oblongata obtains its form in a different manner than in the human subject.

In Figure 15 one sees a few scattered ectodermic cells on the border of the medullary wall and Randschleier.

His has demonstrated the great power of migration which these cells possess, and I am inclined to believe that it is simply to this migration, and consequent accumulation, that in the rabbit the tractus solitarius owes its burial, and not to the development of any distinct rhomboidal lip.

A probable lateral root (V), passing in the figure from the mantel layer to the ganglion, should also be noticed.

Finally, I would acknowledge the deep obligation I am under to Prof. C. S. Minot, of Harvard University, and here offer him my most sincere thanks, not only for his kindness in lending me plates of the first six drawings (which were taken from his book), but also for many valuable suggestions which he made as regards the best method of pursuing this investigation, and in giving me his opinion on all the dubious points of diagnosis.

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